식물학회지 제34권 제2호.
Korean J. Bot. 34(2) : 137~144

Ontogeny of Haustorial Xylem in Parasitic Angiosperm *Cuscuta australis* R. Brown

Lee, Kyu Bae and Chai Doo Lee

(Deparlment of Biological Science Education, College of Education, Chosun University, Kwangju and Department of Biology, College of Natural Sciences, Sung Kyun Kwan University, Suwon)

寄生被子植物 실새삼(*Cuscuta australis* R. Brown)의 吸器內 木部의 個體發生

李 圭 培·李 載 斗

(조선대학교 생물교육과, 성균관대학교 생물학과)

ABSTRACT

Xylogenesis of the haustoriuam in the parasitic angiosperm *Cuscuta australis* R. Brown grown on the host plant *Trifolium repens* L. was studied with light microscopy. As the first event indicating the ontogeny of the haustorial xylem, cell divisions occurred in the fascicular and interfascicular regions of the stele of the parasite stem bearing a mature upper haustoriuim, the portion of haustorium external to host organ. The smaller derivatives contained densely stained cytoplasm and prominent nuclei. It confirmed that these dense cytoplasmic derivataives resulted from the division of the previous vacuolated parenchyma cells. As the haustorium had penetrated the host tissue, the cell division activity extended acropetally from the xylem of the parasite stem toward the base of the haustorium through the interfascicular region of the parasite stem. Thus a strand of the dense cytoplasmic cells was established. At the same time, the densely stained cells adjacent to the xylem of the parasite stem began to differentiate into xylary elements. Eventaually, a strand of haustorial xylem was formed acropetally along the way of the cells with increased cytoplasmic density. The acropetal induction of the division activity of parenchyma cells and its haustorial xylogenesis in the stele of the parasite stem was discussed in relation to a possible generation of morphogenetic or hormonal signal which might lead to a specific pattern of haustorial xylogenesis.

INTRODUCTION

Numerous anatomical studies on the structure and development of the haustorium in parasitic angiosperms have suggested that the final stage in haustoiral maturation is the connection between the vascular tissues of parasite and host. Xylem intercontinuity plays a very important role in translocating water and dissolved solutes from the host xylem (Kuijt, 1969, 1977; Tsivion, 1978b).

Peirce (1893) has stated that in *Cuscuta americana* the haustoirum has central procambial cells, in which haustorial xylogenesis begins near the base of the hauastorim and extends to its apex. In *Cuscuta reflexa*, Thomson (1925) and Forstreuter and Weber (1984) have found that lignificatiion of the xylem proceeds from the parasite cells making contact with the host vessels to the xylem of the parasite stem. In the haustorium of *Cuscuta gronovii*, Truscott (1958) has described a central procambial strand and a bidirectional differentiation of haustorial xylem, which proceeds acropetally from the parasite stem along the procambial strand in the haustorium and basipetally from the host xylem to the central procambium. Tsivion (1978a) has reported that cytokinin applied in the early developmental stage of the haustorium in *Cus-*

cuta campestris promotes the growth of the haustorium and the differentiation of its tracheary elements. Tsivion (1978c) has also represented the xylem differentiating near the base of the haustorium, and moreover has claimed that the haustorial xylogenesis proceeds from the hyphal cells to the haustorial base, so that a tracheary bridge is formed. The existence of the xylary continuum was found in *Cuscuta gronovii* (Moss, 1928), *Cuscuta campestris* (MacLeod, 1961), and other parasitic plants (Piehl, 1963; Musselman and Dickison, 1975; Toth and Kuijt, 1977; Nwoke and Okonkwo, 1978). Most of these workers have represented the basipetal differentiation of the haustorial xylem that proceeds from the parasite cells in contact with the host xylem toward the haustorial base. In *Cuscuta odorata*, phloem connection between the parasite and host has been documented (Israel *et al.*, 1980). Dörr (1987, 1990) has reported the absence of procambial strand within the haustorium itself in *Cuscuta odorata* and has noted that the haustorial vascular tissues derived from haustorial parenchyma cells begin to differentiate from the haustorial part nearest the parasite stem toward the haustorial apex.

No detailed anatomical study has so far been made on haustorial xylogenesis in *Cuscuta*, since Kuijt (1977) has pointed out that *Cuscuta* haustorial xylem tracing back to the stem of the parasite has not yet been clearly revealed. Indeed, the *Cuscuta* stem having haustorium has been overlooked in the studies on haustorial xylogenesis by the above all investigators. For this reason, the term 'haustorial xylem' seems to be used as it means literally a xylem strand existing within the haustorium itself. In addition to this difinition, this work suggested that the haustorial xylem must involve the portion of the xylem strand extending from the xylem of the *Cuscuta* stem to the haustorial base. The present study deals with the ontogeny of the haustorial xylem in *Cuscuta australis*.

MATERIALS AND METHODS

Parasitic angiosperm *Cuscuta australis* R. Brown growing on the host plant *Trifolium repens* L. was collected at the campus of the College of Natural Sciences, Sung Kyun Kwan University, Suwon, Republic of Korea, in the summers of 1983 to 1986. The detailed procedures used in this work were described in a previous paper (Lee and Lee, 1989). Material clearings were prepared according to Lersten's method (1967). The specimens were mounted in xylene and were observed with a Leitz Labolux 12 light microscope.

RESULTS

The *Cuscuta* stem bearing haustoria coiled obliquely around the host stem (Fig. 1). The mature upper haustorium with an endophyte primordium, which established an endophyte, i.e., the portion of a haustorium growing within host tissues, developed from the cortex of the parasite stem that had made close contact with the host stem surface (Fig. 2). During this event, a significant structural feature indicating the differentiation of the haustorial xylem first appeared in the stele of the parasite stem (Fig. 2, ST; Fig. 3): cell divisions occurred in the fascicular and interfascicular regions. The resulting derivatives had densely stained cytoplasm with prominent nuclei. The dense cytoplamic cells were smaller in size in cross section, but were elongated in longitudinal view. This feature was visible clearly in longitudinal plane as in Figs. 7 and 8. Because of the cell division activity, externally the parasite stem was seen to be slightly swollen, and internally the phloem tissues displaced from their original position were usually observed; phloem identification in cross section was somewhat difficult. As the endophyte primordium had invaded the host tissues, the cell division activity started from the parasite stele extended further toward the base of the haustorium through the interfascicular regions (Fig. 4). Serial sectioning, cutting transversely the stems of the parasite and the host and longitudinally the haustorium, revealed acropetal differentiation of the haustorial xylem. When the hyphal cells of the endophyte had reached near the host vascular bundle, the densely stained cells adjacent to the xylem of the parasite stem began to differentiate into the xylary elements which served to form a haustorial xylem strand. These elements were characterized by deposition of a typical secondary wall material which looked like black dots on inner surface of the walls in transverse view (Fig. 5). However, radial longitudinal section as in Fig. 8 showed more clearly the wall thickening of the xylary elements. Such xylary differentiation proceeded acropetally along the route of the cells, having increased cytoplamic density, located at the interfascicular region (Fig. 6). By this stage of the haustorial development, the xylary elements differentiated within the haustorium itself did not appeared.

To observe the precise ontogeny of the haustorial xylem, serial sections that simultaneously cut radially, longitudinally, and transversely through the parasite stem, the haustorium, and the host stem, respectively were examined. These sections showed that the haustorial xylem strand also differentiated acropetally to near the epi-

dermal level of the host stem, when the hyphal cells of the endophyte had made contact with the host xylem and phloem (Fig. 7). In the stele of the parasite stem where the endophyte had established, phloem tissues were usually displaced from their original position (Fig. 7, X, P, and FR), because of the cell division activity in the stele. The dense cytoplasmic cells positioned between xylem and phloem in the stele of the parasite stem also differentiated into the xylary elements forming the haustorial xylem strand. The xylem strand was usually tortuous and thus did not lie in a single sectional plane: each section showed the discontinuity of the xylem strand in the region reaching mainly from the parasite stem's stele to the haustorial base (Figs. 7-9). The xylary discontiniuty at the lower portion of the xylem in the fascicular region in Fig. 7 was supplied in one of the following sections (Fig. 8). The remaining discontinuities, which were seen at the levels corresponding spacially to the upper portion of the phloem in the fascficular region and the haustorial base in Fig. 7, were supplied in another section cutting through the interfascicular region of the parasite stem (Fig. 9).

On the other hand, the optical sections from the cleared materials showed the haustorial xylem bridge differentiation acropetally from the xylem of the parasite stem toward the host leaf (Fig. 10, HL), and stem (Fig. 11, HS) through the haustorial base. 30-cleared and 20-serial sectioned materials were examined to observe the differentiation pattern of the haustorial xylem: 21 specimens of them revealed acropetal differentiation, whereas basipetal manner was not found; in the remaining specimens the xylem bridge between the parasite and host were connected completely. The mature haustorial xylem was usually funnel-shaped.

DISCUSSION

As the mature upper haustorium developed from the cortex of the *Cuscuta australis* stem making close contact the host surface, cell divisions did occur in the fascicular and interfascicular regions of the stele in the parasite stem. The cell division activity extended toward the haustorial base through the interfascicular region of the parasite stem. The smaller derivatives had increased cytoplamic density and conspicuous nuclei. This anatomical structure seems to be the first finding in the study on the haustoiral xylogenesis of *Cuscuta*. We confirmed that these dense cytoplasmic cells apparently derived from the division of the vacuolated parenchyma cells, since the latter comprises the fascicular and interfascicular regions in the stele of the parasite stem devoid of haustoria before contact with the host (Lee and Lee, 1989, Figs. 4 and 5) and also comprises the haustorial base after the haustorium develops (Lee and Lee, 1989, Fig. 9). Such a dedifferentiation pattern of parenchyma cells occurs in the earlier developmental stage of the upper haustorium of *C. australis*, in which close contact between the parasite and the host induces the division activity of the middle-layered, cortical parenchyma cells in the parasite stem, resulting in the initials of an upper haustorium and its maturation (Lee and Lee, 1989). The division of parenchyma cells and its xylary differentiation has also been reported in wound regeneration of *Coleus* pith (Sinnott and Bloch, 1945) and petiole (Jacobs, 1952) and in tissue cultures of lilac callus (Wetmore and Rier, 1963), pea root cortex (Sachs, 1968; Phillips and Torrey, 1973), lettuce pith (Dalessandro and Roberts, 1971), and tobacco pith (Clutter, 1960; Sussex *et al.*, 1972).

The secondary wall material began to deposite in the dense cytoplasmic cells adjacent to the xylem of the parasite stem. By this stage of haustorial growth, the secondary wall thickening could not observe in any cells or tissues consisting the haustorium itself, i.e., not in the haustorial base or apex. On the other hand, the xylary elements first appearing in the haustorial base have been reported in *C. americana* by Peirce (1893) and *C. campestris* by Tsivion (1978c); however, they did not state whether the results were obtained from serial sectioning, and their figures do not involve the *Cuscuta* stem. We also observed xylary elements appearing in the haustorial base from one of the serial sections as in Fig. 9, however, these elements were completely connected spacially to those of the following sections. We conclude that the haustorial xylem began to differentiate acropetally from the dense cytoplasmic cells adjacent to the xylem of the parasite stem; the differentiation proceeded toward the haustorial base through the interfascicular region.

Our observation of acropetal differentiation of haustorial xylem, extending from the stele of the *Cuscuta* stem toward the haustorial base, appears to be the first since basipetal differentiation in *C. reflexa* (Thomson, 1925; Forstreuter and Weber, 1984) and *C. campestris* (MacLeod, 1961; Tsivion, 1978c) and bidiretional differentiation in *C. gronovii* (Truscott, 1958) have been observed within the haustorium itself. Acropetal haustorial xylem maturation described by Truscott (1958) is similar to our result, but its ontogenetical anatomy was not dealt. Dörr (1987) also noted that the differentiation of the haustorial vascular tissues begins at the *Cuscuta* shoot, where that portion seems to correspond to the haustorial base here,

but she did not represent the anatomical structure of the parasite stem. We have not examined here whether the haustorial xylem part extending from the haustorial base toward its apex was derived from procambial cells as in *C. americana* (Peirce, 1893) and *C. gronovii* (Truscott, 1958) or from haustorial parenchyma cells as in *C. odorata* (Dörr, 1987, 1990). The acropetal haustorial xylogenesis has been stated in many other parasitic members (Stephens, 1912; Maybrook, 1917; Simpson and Fineran, 1970; Chuang and Heckard, 1971). Basipetal xylogenesis in *Cuscuta* haustorium have been interpreted with the concept of cytokinin concentration or transport. The *Cuscuta* haustorium has a lower level of cytokinin as compared with that of the host tissue (Jacob *et al.*, 1975), and thus a high enough cytokinin concentration for the haustorial xylogenesis may be translocated from the host xylem to the parasite (Tsivion, 1978a; Gupta and Singh, 1985). Therefore, the hyphal cells of the endophyte making contact the host xylem begin to differentiate into the xylary elements which proceeds successively to backward, and finally a xylem bridge through haustorium is basipetally formed (Thomson, 1925; MacLeod, 1961; Tsivion, 1978b, c; Forstreuter and Weber, 1984). Such an explanation would be favored only after the endophyte primordium penetrates the host. All workers referring to the haustorial xylogenesis have not attention the *Cuscuta* stem with a mature upper haustorium which had not yet invade the host. We stress here that the appearance of the cell division activity in the stele of the *C. australis* stem was the first event in the acropetal xylogenesis of the haustorium.

Considering that a certain range of hormones may determine a specific pattern of differentiation of plant cells or tissues (Wareing and Phillips, 1981), our result showing the acropetal direction of the division activity of parenchyma cells and its xylogenesis in the *Cuscuta* stem's stele leads to us the following conclusion: a gradient of hormone concentration had already been established for the acropetal pattern before the endophyte primordium penetrates the host tissues. For this to be operated, one must assume that a morphogenetic signal (Kuijt, 1983) starts to flow from the xylem of the *Cuscuta* stem, not from the host, although no biochemical evidence on the hormone exists. To explain a possible induction of the acropetal division activity of parenchyma cells and its haustorial xylogenesis, one must consider how the morphogenetic signal which may operate the acropetal mode originates before the intrusion of the endophyte primordium.

The xylem of the *Cuscuta* stem may contain a natural cytokinins and auxins which act in the initiation of cell division and xylogenesis (Roberts, 1976). So it is conceivable that the vacuolated parenchyma cells adjacent to the parasite xylem began to divide. This dedifferentiation could establish a strand of the densely stained cytoplasmic cells like here along the flow of the hormonal signal. Simultaneously, an autolysis as cellular breakdown may take place in precusors of the xylary elements like the smaller cells with dence cytoplasm here, thus auxin would be produced by the differentiating xylem itself (Schedrake, 1973). Eventually, those hormones might stimulate to cause so-called homeogenetic induction: a differentiation pattern in one cell or tissue may induce similar manner adjacent cell or tissue (Cutter, 1978; Wareing and Phillips, 1981). Therefore, we would suggest that the morphogenetic or hormonal signal began to flow from the xylem of the *Cuscuta australis* stem and played some role in directng the acropetal homeogenetic induction of the division activity of parenchyma cells and its haustorial xylogenesis. Comparative study of biochemistry on hormones known to affect the specific plant cells or tissues with its corresponding anatomy would be helpful to better understand the ontogeny of haustorial xylem.

적 요

기주식물(토끼풀, *Trifolium repens* L.)에 기생하는 실새삼(*Cuscuta australis* R. Brown)의 흡기내 목부의 개체발생 과정을 광학현미경으로 조사하였다. 흡기의 목부 분화를 암시하는 최초의 해부학적 특징이, 흡기 자체내에서가 아니라, 그 흡기가 형성되어 있는 실새삼 줄기에서 나타났다. 즉 실새삼 줄기의 중심주의 유관속 내부 및 유관속 사이에서 세포분열 활성이 관찰되었다. 이 분열로부터 유도된 세포들은 짙게 염색된 세포질과 뚜렷한 핵을 갖고 있었다. 흡기가 기주조직에 침입하여 생장함에 따라, 실새삼 줄기의 중심주에서 시작된 세포분열 활성은 유관속 사이를 거쳐서 흡기의 기부를 향하여 구정적으로 확장되었다. 이와 동시에, 실새삼 줄기의 목부에 인접해 있던, 짙은 세포질 밀도를 갖는 세포들이 목부요소로 분화하기 시작하였다. 결국, 이미 형성되었던 짙게 염색된 세포들을 따라서 흡기의 목부는 구정적으로 분화하였다. 실새삼 줄기의 중심주에서 일어나는 유조직 세포들의 분열활성 및 이로부터 흡기의 목부 분화를 구정적으로 유도할 수 있는 가능성에 대하여 논의하였다.

REFERENCES

Chuang, T.I. and L.R. Heckard. 1971. Observations on root-parasitism in *Cordylanthus* (Scrophulariaceae). *Am. J. Bot.* **58**: 218-228.

Clutter, M.E. 1960. Hormonal induction of vascular tissue in tobacco pith in vitro. *Science* **132**: 548-549.

Cutter, E.G. 1978. Plant anatomy. Part I. Cells and tissues. 2nd ed. Edward Arnold.

Dalessandro, G. and L.W. Roberts. 1971. Induction of xylogenesis in pith parenchyma explants of *Latuca*. *Am. J. Bot.* **58**: 378-385.

Dörr, I. 1987. The haustorium of *Cuscuta*-new structural results. *In*, H.C. Weber and V.W. Forstreuter (eds.), Proceedings of the 4th International Symposium on Parasitic Flowering Plants, Marbrug, FRG. pp. 163-170.

Dörr, I. 1990. Sieve elements in haustorium of parasitic angiosperms. *In*, Sieve Elements-Comparative Structure, Introduction and Development, H.D. Behnke and R.D. Sjolund (eds.). Springer-Verlag, Heidelberg. pp. 239-256.

Forstreuter, V.W. and H.C. Weber. 1984. Zum Parasitismus von *Cuscuta* auf *Euphorbia*-Wirten. *Beitr. Biol. Pflanzen* **59**: 31-54.

Gupta, A. and M. Singh. 1985. Mechanism of parasitism by *Cuscuta reflexa*: Distribution of cytokinins in different regions of the parasite vine. *Physiol. Plant.* **63**:76-78.

Israel, S., I. Dorr and R. Kollmann. 1980. Das Phloem der Haustorien von *Cuscuta*. *Protoplasma* **103**: 309-321.

Jacob, F., U. Strobel, L. Engelbrecht, and W. Schulz. 1975. Studien an *Cuscuta reflexa* Roxb. III. Zur Frage einer cytokininabhanigen Nahrstoffaufnahme. *Biochem. Physiol. Pflanz.* **168**: 349-359.

Jacobs, W.P. 1952. The role of auxin in differentiation of xylem around wound. *Am. J. Bot.* **29**: 301-309.

Kuijt, J. 1969. The biology of parasitic flowering plants. University of California Press. Berkeley and Los Angeles.

Kuijt, J. 1977. Haustoria of phanerogamic parasites. *Ann. Rev. Phylopathol.* **17**: 91-118.

Kuijt, J. 1983. Tissue compatibility and haustoria of parasitic angiosperms. *In*, Vegetative compatibility responses in plants, R. More (ed.). Baylor University Press, Waco, Texas. pp. 1-12.

Lee, K.B. and C.D. Lee. 1989. The structure and development of the haustorium in *Cuscuta australis*. *Can. J. Bot.* **67**: 2975-2982.

Lersten, N.R. 1967. An annotated bibliography of botanical clearing methods. *Iowa State J. Sci.* **41**: 481-486.

MacLeod, D.G. 1961. Some anatomical and physiological observations on two species of *Cuscuta*. *Trans. Bot. Soc. Edinb.* **39**: 302-315.

Maybrook, A.C. 1917. On the haustoria of *Pedicularis vulgaris* Tournet. *Ann. Bot.* **31**: 499-511.

Moss, E.M. 1928. The haustorium of *Cuscuta gronovii*. *Phytopathology* **18**: 478.

Musselman, L.J. and W.C. Dickison. 1975. The structure and development of the haustorium in parasitic Scrophulariaceae. *Bot. J. Linn. Soc.* **70**: 183-212.

Nwoke, F.I.O. and S.N.C. Okonkwo. 1978. Structure and development of primary haustorium in *Alectra vogelii* Benth (Scrophulariaceae). *Ann. Bot.* **42**: 447-454.

Peirce, G.J. 1893. On the structure of the haustoria of some phanerogamic parasites. *Ann. Bot.* **7**: 291-327.

Phillips, R. and J.G. Torrey. 1973. DNA synthesis, cell division and specific cytodifferentiation in cultured pea root cortical explants. *Devl. Biol.* **31**: 336-347.

Piehl, M.A. 1963. Mode of attachment, haustorium structure, and hosts of *Pedicularis canadensis*. *Am. J. Bot.* **50**: 978-985.

Roberts, L.W. 1976. Cytodifferentiation in plants. Xylogenesis as a model system. Cambridge University Press.

Sachs, T. 1968. On the determination of the pattern of vascular tissues in peas. *Ann. Bot.* **32**: 781-790.

Scheldrake, A.R. 1973. The production of hormones in higher plants. *Biol. Rev.* **48**: 509-559.

Simpson, P.G. and B.A. Fineran. 1970. Structure and development of the haustorium in *Mida salicifolia*. *Phytomorphology* **20**: 236-248.

Sinnott, E.W. and R. Bloch. 1945. The cytoplasmic basis of intercellular patterns in vascular differentiation. *Am. J. Bot.* **32**: 151-156.

Stephens, E.L. 1912. The structure and development of the haustorium of *Striga lutea*. *Ann. Bot.* **26**: 1067-1076.

Sussex, I.M., M.E. Clutter and M.H.M. Goldsmith. 1972. Wound recovery by pith cell redifferentiation: structural changes. *Am. J. Bot.* **59**: 797-804.

Thomson, J. 1925. Studies in irregular nutrition. No. 1. The parasitism of *Cuscuta reflexa* Roxb. *Trans. Roy. Soc. Edinb.* **54**: 343-356.

Toth, R. and J. Kuijt. 1977. Anatomy and ultrastructure of the haustorium in *Comandra* (Santalaceae). *Can. J. Bot.* **55**: 455-469.

Truscott, F.H. 1958. On the regeneration of new shoots from isolated dodder haustoria. *Am. J. Bot.* **45**: 169-177.

Tsivion, Y. 1978a. Possible role of cytokinins in nonspecific recognition of a host and in early growth of haustoria in the parasitic plant, *Cuscuta campestris*. *Bot. Gaz.* **139**: 27-31.

Tsivion, Y. 1978b. Physiological concepts of the association between parasitic angiosperms and their hosts-A review. *Israel J. Bot.* **27**: 103-121.

Tsivion, Y. 1978c. Host tissue determination of xylem formation in the haustorium of *Cuscuta*. *Israel J. Bot.* **27**: 122-130.

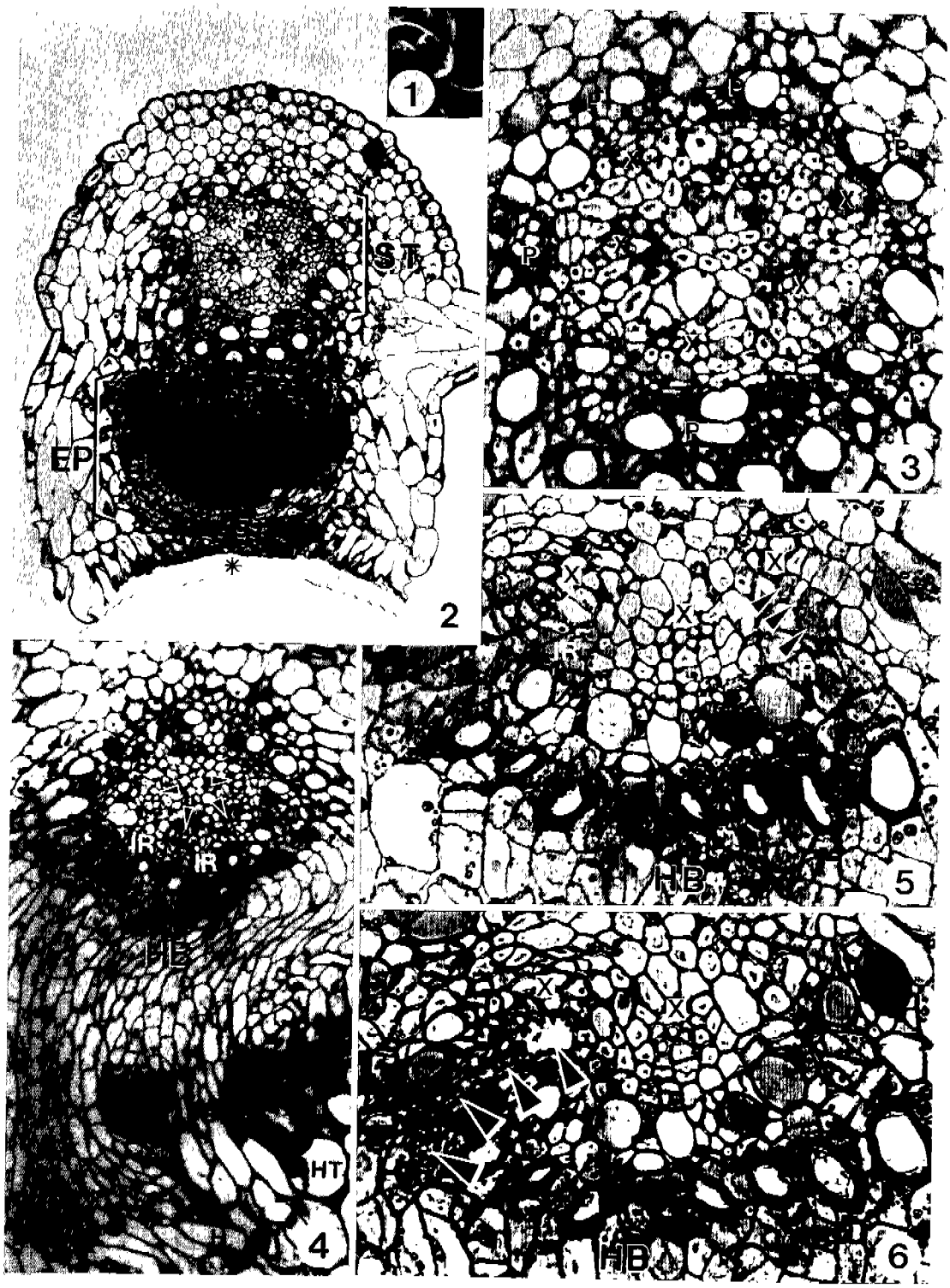
Wareing, P.F. and I.D.J. Phillips. 1981. Growth and differentiation in plants. 3rd ed., Pergamon Press, Oxford.
Wetmore, R.H. and J.P. Rier. 1963. Experimental induction of vascular tissues in callus of angiosperms. *Am. J. Bot.* **50**: 418-430.

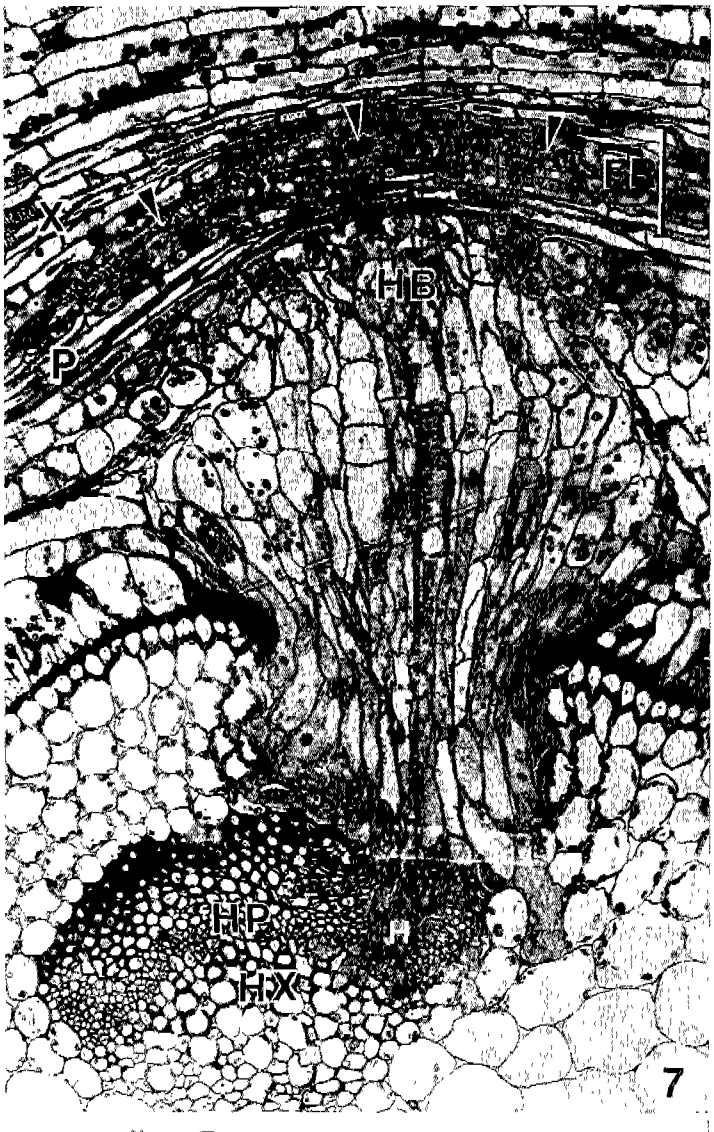
(Received April 8, 1991)

Explanation of Figures

Figs. 1-6. Differentiation of the haustorial xylem in *Cuscuta australis*. Fig. 1. Parasite stem bearing haustoria is coiled obliquely to the length of the host stem. ×1.8. Fig. 2. Fully mature upper haustorium has an endophyte primordium (EP) at the side that contacts the host stem surface (asterisk). Note cell division activity in the stele (ST) of the parasite stem. ×150. Fig. 3. Enlarged view of the stele in Fig. 2 shows that the cell division activity occurred in the fascicular region between xylem (X) and phloem (P), and in the interfascicular region between the vascular bundles. In this cross section, the derivatives of the division are smaller in size and contain more or less dense cytoplasm with nuclei. ×276. Fig. 4. The cell division activity extends toward the haustorial base (HB) through the interfascicular regions (IR) between the vascular bundles. Arrowheads indicate the position of the xylem pole of the parasite stem. H, hyphal cell; HT, host tissue. ×167. Figs. 5 and 6. Two serial cross sections showing acropetal haustorial xylogenesis initiating in the stele of the parasite stem. 5. This section exhibits that secondary wall, looks like black dots, begins to deposite on the wall of the densely stained cytoplasmic cells (arrowheads) adjacent to xylem (X) of the parasite stem. Note the cells, having increaed cytoplasmic density, reaching toward the haustorial base (HB) through the interfascicular region (IR). ×372. 6. A strand of haustorial xylem (arrowheads) extending acropetally from the cells adjacent to the xylem (X) of the parasite stem toward the haustorial base (HB). ×372.

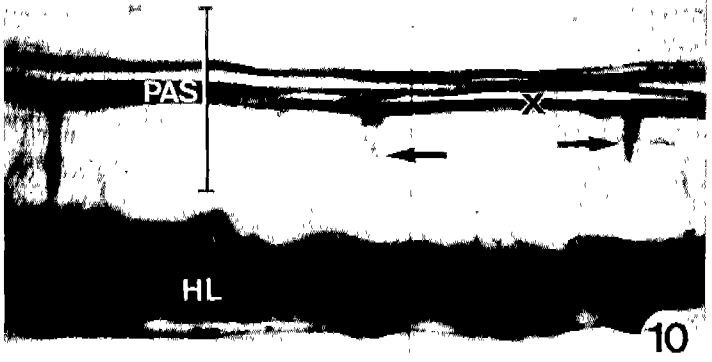
Figs. 7-11. Differentiation of the haustorial xylem in *Cuscuta australis*. Figs. 7-9. Serial sections in radial longitudinal plane showing acropetal haustorial xylogenesis. Fig. 7. In the parasite stele, the elongate, dense cytoplasmic cells located in the middle portion of the fascicular region (FR) between the xylem (X) and the phloem (P), differentiate into xylary elements (arrowheads). Xylem discontinuities and seen at the haustorial base (HB), and at the upper and lower portions of the phloem and the xylem, respectively. H, hyphal cell; HP, host phloem; HX, host xylem. ×250. Fig. 8. The dense cytoplasmic cells adjacent to the xylem (X) of the parasite stem differentiate into the xylem elements (arrowheads) which supply the xylem discontinuity that was seen at the lower portion of the xylem in Fig. 7. ×250. Fig. 9. The xylary elements (arrowheads), which differentiated from the densely stained cytoplasmic cells positioned at the interfascicular region (IR), supply xylem discontinuities that were seen in Figs. 7 and 8. HB, haustorial base. ×250. Figs. 10 and 11. Optical sections from cleared materials show that the haustorial xylems (arrows) differentiated acropetally from the xylem (X) of the parasite stem (PAS) toward the host leaf (Fig. 10, HL) and stem (Fig. 11, HS). Note the point of the arrows indicates the haustorial base3. ×134. ×111.

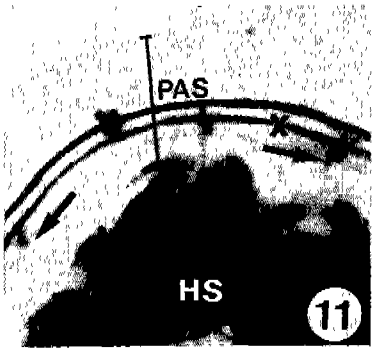

1
ST
EP
2
P
X
3
IR
HB
5
HT
4
6


X
FB
HB
P
HP
H
HX
7


X
HB
8


FB
HB
9


PAS
X
HL
10


PAS
X
HS
11